

Units of Interaction, Evolution, and Replication: Organic and Behavioral Parallels

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Organic and behavioral evolution both involve variation, selection, and replication with retention; but the individuals involved in these processes differ in the two kinds of evolution. In this paper, biological units of evolution, selection, and retention are compared with analogous units at the behavioral level. In organic evolution, natural selection operates on variations among organisms within a species, with the result of preserving in future generations of organisms those heritable characteristics that contributed to the organism's survival and reproduction. Species evolve as characteristics of the population change as a result of past selection. Continuity in a lineage in the biosphere is maintained by replication of genes with retention of organismic characteristics across successive generations of organisms. In behavioral evolution, reinforcement operates on variations among responses within an operant, with the result of preserving in future responses those characteristics that resulted in reinforcement. Continuity in a behavioral lineage, within the repertoire of a given organism, appears to involve retention and replication, but the unit of retention and replication is unknown. We suggest that the locus of retention and replication is the nervous system of the behaving organism.

Key words: operants, evolution, selection, variation, replication, retention, behavioral units

Reinforcement and natural selection were first discussed over four decades ago as parallel processes operating in two different scientific domains (e.g., see Campbell, 1956; Skinner, 1953). Skinner further developed his evolutionary theme in papers published in 1981, 1984, and 1986. During the 1990s, theoretical papers in behavior analysis have increasingly explored that theme. Ready evidence can be found in the issue of the *American Psychologist* dedicated to "reflect[ing] on and celebrat[ing] the scientific and intellectual impact of B. F. Skinner on

psychology" (Lattal, 1992, p. 1269). At least six of 23 articles in that issue explicitly addressed parallels between organic and behavioral evolution (Alessi, 1992; Baum & Heath, 1992; Catania, 1992; Chiesa, 1992; Glenn, Ellis, & Greenspoon, 1992; Palmer & Donahoe, 1992). Despite that commonality, each of the six articles (and Ringen, 1993, as well) dealt with entirely different issues—testimony to the richness of the subject and the complexity of those issues.

In this paper we further explore possible parallels between concepts in behavior analysis and concepts in organic evolutionary theory. Specifically, we consider units in the behavioral domain that parallel the units of organisms, species, and genes in organic evolutionary theory. Our strategy is to make use of recent work in the philosophy of biology to examine ontogenic behavioral phenomena as a function of ontogenic processes of selection, interaction, and retention that parallel those same kinds of processes in organic evolution. Concepts in evolutionary biology are undergoing intense scrutiny by both biologists and philosophers of

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biology who are sorting out conceptual muddles that have plagued evolutionary theory since its inception (see, e.g., Ghiselin, 1974; Hull, 1989; Mayr, 1982; Sober, 1984). The work of those and other biologists and philosophers of biology may aid behavior analysts in exploring comparable issues in their own domain.

Readers might reasonably ask "Why? What is the purpose of this exercise?" One reason is that some of the most profound issues in behavior analysis have not been addressed in ways that have led to a continuously developing explanatory framework. Some of the most insightful explorations of the concept of the operant (e.g., Catania, 1973; Schick, 1971) do not readily lend themselves to understanding the complexity that appears to characterize human behavioral repertoires. Because evolutionary theory has been highly successful in explaining organic complexity, and because ontogenic behavior is seen increasingly as a product of selection processes of a second kind, the explanatory structure of evolutionary theory could provide guideposts for developing a theoretical framework of similar power. The present effort is an attempt to examine some basic concepts from a different angle—one that is not inherently inconsistent with previous views but that could lead to examining those views from a new and useful perspective.

Another reason for pursuing the topic is that viewing old concepts from a new perspective can stimulate new approaches to research and application. Such has been the case in other sciences. New vocabularies, or at least revised meanings for old terms, can have a liberating effect on thinking, fostering reexamination of assumptions and accepted definitions. Systematic reexamination of that kind could lead, as it has in evolutionary biology, to solutions to some long-standing conceptual impasses. In addition, it might foster new measurement procedures, methods, or environmental manipulations.

Finally, if organic evolution and be-

havioral evolution involve the same kinds of processes, explication of those processes in either domain could provide insight into recalcitrant problems in the other. This would be true even if the two domains were not substantively related to one another, as they are in the case of organic and behavioral evolution. Whether or not the present effort has any such direct effects is less important to us than that it contribute to the process of reexamination.

SOME GENERAL POINTS

The experimental analysis of behavior has sought from its inception to formulate principles that describe lawful relations between the behavior of organisms and other observable events (Skinner, 1938). Those principles, like the principles of other sciences, are generalizations that are content free (cf. Lee, 1988). For example, the principle of reinforcement describes a certain kind of relation that can be observed at the behavioral level. Specifically, the relation entails two parts—a response–consequence contingency and a resulting increase in the rate of the responding followed by that consequence. The principle does not specify any particular activity or any particular consequence. It is "a generalization that [is] spatiotemporally unrestricted [and] that refers to any entities that happen to have the appropriate characteristics" (Hull, 1984, p. 145). The appropriate characteristics in the case of the reinforcement principle are behavior–consequence relations that are functionally related to increased rate of responding.

Accounting for observed phenomena in terms of such principles is one kind of scientific explanation. For example, if we observe that a parent attends when a child is whining but not when whining is absent, and we note that the whining increases in frequency, we explain the high rate of whining by invoking the principle of reinforcement. Such explanation is structurally

similar to the invocation of the principle of natural selection to account for the fact that humans are bipedal organisms with opposable thumbs.

Only behavioral content that is acquired during the lifetime of individual organisms requires principles beyond those that account for the existence of a given species and its constituent organisms. Principles that account for the existence of species and characteristics of their constituent organisms include the principles of evolutionary biology. Because it is organisms that behave, the principles of evolutionary biology clearly have some bearing on their behavior; indeed, sociobiologists have attempted to account for behavioral content of individual organisms (including humans) with those principles (e.g., Wilson, 1975). However, sociobiologists (e.g., Dawkins, 1976; Wilson, 1975) also appear to agree that much human behavior cannot be attributed directly to the processes of organic evolution. Rather, the specific behavior of each human depends on what events occur during that human's lifetime (Dawkins, 1976). At this point, sociobiological theory becomes more a matter of lay intuition than scientific formulation.

It is not necessary, however, to rely so heavily on intuition, because progress has been made in accounting for behavior that is not directly attributable to organic evolutionary processes. The account makes use of principles pertaining to ontogenic processes that involve evolution of another kind (Campbell, 1956; Skinner, 1953; Staddon, 1973). These ontogenic processes are themselves products of organic evolution, but they operate in the domain of behavioral evolution. The evolution of behavior during the lifetime of an individual organism has been called *behavioral evolution* to distinguish it (and its causal processes) from organic evolution (and its causal processes) (Glenn & Field, 1994).

In this paper, we attempt to draw out parallels between behavioral entities and the entities involved in organic

evolution. We hope readers will not conclude with undue haste that *behavior* and *entity* are fundamentally mismatched terms. To be sure, the entities involved in behavioral evolutionary processes (e.g., responses and operants) are functional properties of organisms. But they do have properties that can be measured, and within the context of a given organism, complex relations among them may constitute a behavioral system that is often referred to as a *repertoire*. If comparisons to organic evolutionary concepts are to be made, it is convenient to have a common term for all the individuals of interest. *Units* would often do as well as *entities*, and we shall use the two terms interchangeably in order to continually remind readers (and ourselves) that units of behavior in a repertoire have roles in the explanatory structure of behavior analysis similar to the roles of various entities in the explanatory structure of organic evolutionary theory.

In the sections that follow, we first briefly review some of the issues under discussion in evolutionary biology regarding the concept of selection. In the three remaining sections we take up, in turn, the units of interaction, evolution, and replication in the two kinds of evolutionary processes.

SELECTION AND ORGANIC EVOLUTION

Organic evolutionary theory is replete with concepts that have been defined differently at different times and by theorists of different persuasions. For example, controversy abounds with respect to the definition of *fitness* and what the role of that concept is (or should or shouldn't be) in evolutionary theory (see Beatty, 1992, Keller, 1992, and Paul, 1992, for discussion from three perspectives in a single volume). Our reading of the literature, admittedly selective, leads us to avoid dealing with the term. As an aside, we note that Mayr's classic text, *The Growth of Biological Thought* (1982), indexes the

word as appearing on only 3 of 858 pages. In a later text (in which *fitness* appears on 4 of 550 pages), Mayr seems to accept what "the average person knows" about its meaning: "It is the capacity of an organism to survive in a given environment or, in other words, to cope with the conditions of the environment" (Mayr, 1988, p. 128). Sober (1984) spends 225 pages disentangling fitness from the causal structure of selection processes in evolutionary theory. The result of that endeavor is an analysis of selection as a causal process, whereas "fitness is causally inert" (p. 85), as he suggested at the outset of the discussion.

Most theorists view natural selection as accounting "for the *origin* as well as the *spread* of new variants or traits" (Endler, 1992, p. 220, italics in original). Three conditions define the process of natural selection: variation in some attribute of individuals that are members of a natural population; a consistent relationship between that attribute and survivorship, mating ability, or both; the attribute must be capable of being passed on to future individuals (inherited) (Endler, 1992).

One of the topics of ongoing debate in evolutionary biology has to do with the level at which selection occurs. The question typically posed is "What is the unit of selection?" The main contenders are genes, organisms, and populations (Brandon & Burian, 1984), and the proponents of the various answers seem to have had no success in persuading one another to change their views. Philosophers of biology and philosophically inclined biologists attribute the recalcitrance of the problem to other unsolved definitional issues, particularly the definition of *selection*. Hull (1989, chap. 6) suggested that selection involves two different kinds of entities: replicators and interactors. A replicator is "an entity that passes on its structure largely intact in successive replications," whereas an interactor is "an entity that interacts as a cohesive whole with its environment in such a way that this interaction causes repli-

cation to be differential" (Hull, 1989, p. 96). Hull concluded that "genes are obviously the most fundamental replicators [in organic evolution]" (p. 98). In organic evolution, organisms are always interactors (but not necessarily the only organic entities that interact with their environment). Hull's distinction between replication and interaction is a distinction of function. He seems to be saying that selection processes (in the organic domain or any other) involve entities with replicating functions and entities with interacting functions (and some entities may function both ways). Proponents of genic selection emphasize the role of replication in natural selection. Biologists who are convinced that the organism is the unit of selection emphasize the interaction between organism and environment that determines whether or not genes are replicated in the next generation. In short, Hull attributes their disagreement to a difference in proclivities for focusing on either replication or interaction in the selection process.

In sorting out the ways in which the term *selection* is used in evolutionary theory, Sober (1984) made another distinction, different from Hull's but not incompatible. Sober distinguished between selection of objects and selection for properties. He used a child's toy to develop an analogy to explain that distinction. The toy is a transparent cylinder with several compartments separated by horizontal filters, each having successively smaller holes in it than the one above. In the top compartment are a number of balls of different size, each size having a particular color. Shaking the cylinder results in all the green middle-sized balls and the red small balls moving into the middle compartment, while the large blue balls remain in the top compartment. Further shaking results in only the red small balls moving into the lowest compartment. The smaller the balls, then, the more successful they are at reaching the bottom compartment (surviving).

Sober (1984) uses this analogy to

point out that small red balls were the objects selected (i.e., their numbers increased proportionally in the population), and that they were selected for their property of smallness. Their property of redness was also selected, but the balls were not selected for that property. Thus, what survives the selection process is not only what was selected *for* but also all other heritable properties of the objects *of* selection. Natural selection, then, involves the selection of organisms (phenotypes); and it involves selection for those (genetic) characteristics that match the selecting environment well enough to result in replication of the genes in the next generation.

BEHAVIORAL UNITS OF INTERACTION

Responses are the entities in the behavioral domain that are the counterpart of organisms in the organic domain. We use *response* here as Skinner sometimes used it—as a single instance of behavior. A response includes an activity component and an effect component (Glenn et al., 1992; Glenn & Field, 1994). Here it means the same thing as a “thing done” (Lee, 1994). A response, which exists in the behavioral domain, is parallel to an organism in the organic domain, at least with respect to evolutionary processes. Organisms and responses are the concrete particulars of everyday observation (cf. Lee, 1988). Responses are also the entities of practical interest to humans, and “the probability of a *single forthcoming event*” is that for which behavior-analytic principles ultimately are designed to account (Skinner, 1957, p. 28, original italics).

Like organisms, responses are interactors par excellence. Responses come into direct contact with the selecting environment. They are the phenotypes of behavioral evolution. Differences among their attributes provide the variation that allows for differential selection. The importance of variation among phenotypes in selection pro-

cesses returns us to Sober’s (1984) distinction between “selection of” and “selection for.” A similar distinction can be made in behavioral evolution. Consider that the natural selection process occurs via the match or mismatch between characteristics of organisms and the selecting environment. So too does the operant conditioning process occur as differential environmental events follow individual responses having different properties, only some of which result in the required match. Consider a rat’s existing lever-pressing operant. It can be described in terms of numerous physical and dynamic properties. Some of those properties are required for reinforcement, and some are not. Responses having the required properties result in reinforcement, and future responses are more likely to have those properties. Future responses are also more likely to have properties of the reinforced responses that were not required (Mechner, 1992). There has been selection of certain responses and all of their properties and selection for the response properties meeting requirements of the contingency. The properties of later responses are likely to stabilize around certain values if the same contingencies remain in force.

UNITS THAT EVOLVE

In biological evolutionary theory, species are considered to be units of evolution (Brandon & Burian, 1984). Natural selection is said to account for the origin of species (Darwin, 1859/1958) as well as for changes in species characteristics over time. Natural selection is a creative (albeit blind) process (Dawkins, 1986) because it accounts (but not by itself) for the forms and functions of existing species.

From the Greek period until Darwin, organisms were considered to be conforming (with greater or lesser fidelity) to the universal essence of their type; the various types were named as species. Variation within the type was a kind of “error”—a straying from the true nature of the type. This perspec-

tive has been called the *essentialist* concept of species and contrasted with the *biological* concept of species (Mayr, 1982), which views a species as a chunk of an evolving lineage that has internal coherence. All organisms belonging to a species are descended from a common ancestor, which is the source of the internal coherence of that species.

A species is composed of a single population of organisms or a population of populations. The term *population* is used in many ways, including as "a collection of individuals of any sort characterized by the distribution of one or more traits of those individuals . . . [but] . . . the populations that function in the evolutionary process are populations in a much more restricted sense of the term. *Descent is required*" (Hull, 1989, p. 85, emphasis added). This restricted meaning of population is what is meant here by the term *natural population*. It is used to restrict the designated population to one with members that belong to that population by virtue of their common descent (whether or not humans classify them as so belonging). In sexually reproducing organisms, the effect of this shared history generally is that only those organisms that share that history have homologous chromosomes (i.e., have the same or corresponding features; Mayr, 1982) and can thus play a role in maintaining the lineage by propagating.

Species, then, are organic evolutionary units. They are natural populations with members that are distributed across space at any particular time, and across time that spans multiple generations. Evolution occurs in the time dimension and can be seen only in changes over time in the distribution of population characteristics; however, its effects can be seen in differences among members of subpopulations at a particular period in time. The members of an extant biopopulation have species-specific characteristics that differ in their values from one organism to another. For example, humans are each

equipped with a larynx. The vocal cords therein vary in length and thickness from one individual to another, accounting for some of the differences observed among human voices. Features of the environment in which the organisms exist are generally matched with the properties characterizing the population (as a result of previous selection). But the differing values of the properties of individual organisms result in differential matches, and those organisms having properties better matched to current environments are thereby selected. It seems possible that the larynx evolved in humans via differential selection of those humans who could make a greater variety of sounds. Because a fairly large range of thicknesses met the survival contingencies, the variation remained and may even have increased, while the contingencies selected for the general form of the organ.

Having identified the unit of organic, or phylogenetic, evolution and some characteristics of that unit, we now turn to the analogous unit at the level of behavioral, or ontogenic, evolution. That unit is the operant. Behavior analysts use terminology that is slightly different but analogous to that of evolutionary biologists when they describe the operant as a unit of analysis. In saying that the operant is the unit of analysis in behavioral evolution, we are saying that operants are the entities whose existence behavioral evolutionary theory must account for. This gives rise to the following question: Why is it that operants must be accounted for when it is particular responses (in their infinite variety) that most people are ultimately interested in? There seem to be many related answers to this question, some of which will be considered in this section. The short answer is that particular responses are possible because of the reinforcement history of the operant of which they are a part. Reinforcement accounts for the origin of operants in the repertoire of a particular organism, changes in their characteristics over time, and the ontogenic

functions of environmental events with respect to ongoing behavior. To understand any particular response, we must understand the contingencies of reinforcement that gave rise to the evolutionary unit of which it is an instance and also to the instantiating functions acquired by environmental events during a particular behavioral history (Glenn & Field, 1994).

Just as a species is a population of organisms, an operant is a population of responses. Although "population thinking" is likely to be as important for behavioral evolutionary theory as it has been for organic evolutionary theory, it is a difficult concept as applied to behavior for a number of reasons. First, "population" has been associated with "organisms" in the history of most people; thus, its application to behavioral events may seem odd to many readers. A second reason for the difficulty is that the population of responses constituting an operant is distributed only in time, whereas the population of organisms constituting a species has concurrently existing members. That is, members of a species are distributed horizontally in space as well as vertically in time (cf. Mayr, 1982). Objects that may all be observed at one time are easier to view as a population than are events that occur at nonoverlapping times. Third, the members of operant populations (dated instances of action) have a fleeting existence (from the human perspective); although they can be pointed to, they cannot be touched or held onto, whereas the term *population* often specifies a number of tangible objects.

Despite those difficulties, the concept of the operant as a population may be as important to behavior analysis as the concept of a species as a population has been to organic evolutionary theory. Indeed, most measures of operant behavior are population measures. *Rate*, the standard measure of an operant, is a population measure. The cumulative record is a graphic display of the distribution in time of a population of responses. Measures of central ten-

dency, such as mean interresponse time, are often used in mathematical descriptions of operant units. In the matching law, subpopulations of an operant are functionally related to characteristics of their own niche as well as to the characteristics of the other subpopulation. Even so, the relevance of population thinking to behavior-analytic theory has only recently begun to be explicated in an evolutionary context (e.g., Baum, 1994; Glenn et al., 1992).

As in the case of species, operants are not defined in terms of the similarity of individual members of the population to one another. A particular operant is a population of responses with a common origin—a specific reinforcement history. For example, a rat's lever-pressing operant may be shaped from behavioral variability by the experimental contingencies. The rat's subsequent lever presses may not all look the same, but they are all members of the same operant because they are products of a common history of selection by reinforcing consequences. Similarly, all individual members of a species are the products of a common history of natural selection, even though any two may not look alike.

Ghiselin (1974) has argued, with increasing agreement from other theorists and philosophers of biology, that a particular species is not only a population but is also an individual. That is, a species is a unit with ontological status and is not a construct with no counterpart in the physical universe. A species exists as an historical (albeit often changing) entity; it is as "real" as a particular organism, which is also an historical and continuously changing entity. The correct logical relation between a species and its constituent organisms is whole to part (Ghiselin, 1974), and both the species and its organisms are individuals. Conceiving of an individual entity with parts that appear not to be spatially and temporally contiguous with one another is difficult; but the spatial and temporal contiguity of cells in an organism would

not be apparent to a being the size of an atom.

An operant, like a species, exists as an historical entity. Skinner specified its ontological status like this:

It is not necessary to assume specific identifiable units prior to conditioning, but *through conditioning they may be set up. I shall call such a unit an operant* and the behavior in general operant behavior. (Skinner, 1937/1972, pp. 491–492, emphasis added)

Thus, an operant is an entity (unit) that is accounted for in terms of historical (conditioning) events that had particular dimensions and characteristics. An operant (like a species), then, is an individual that exists in the natural universe and is composed of parts (response instances) that constitute a natural population that is distributed in time. The population comprising a particular individual operant is a population of responses. As Lee (1988) put the case, each response (act) can be specified to exist at a particular spatio-temporal location. The particular operant of which those responses are a part is also a spatiotemporally localized individual. It is part of a particular organism's repertoire, just as *Homo sapiens* is part of a particular biosphere.

An individual operant is localized with respect to the particular organism's repertoire of which it is a part; it has a beginning (albeit sometimes a fuzzy boundary) and an end (perhaps in extinction of the operant or perhaps in death of the organism). The parts of any particular operant are distributed in space and time, and are not contiguous with one another but often interspersed among other behavioral units in the behavior stream of a particular organism (Glenn & Field, 1994). But, as in the case of a particular species, an operant is still an historical entity.

Also as in the case of a species, there may be no exact moment at which an operant can be said to begin. An operant evolves from the organismic activity on which selection operates: It is part of a lineage, as is a species. A particular operant may evolve

from the uncommitted behavior of the newborn (as some species are said to have evolved from the primeval ooze); other operants emerge, under certain conditions, from earlier operants that are already in an organism's repertoire. Individual species are entities that evolve in organic lineages as part of the Earth's biosphere, and individual operants are entities that evolve in behavioral lineages as part of an individual organism's repertoire.

An operant's characteristics may change if the contingencies are altered. As an example, consider a rat pressing a lever on a fixed-ratio (FR) 1 schedule. The lever pressing evolved from an earlier operant repertoire as a result of selection by reinforcement. The lever pressing constitutes a behavioral unit brought into existence by the process of operant conditioning. The unit is a population of responses having a common origin. If the contingencies don't change for an extended period, then stable population characteristics of the operant will emerge. For example, the individual responses may have a narrow band of force values (say 2 to 5 N) on the lever, hovering around the minimum force required—in this case, say 3 N. If the contingencies are changed so that only responses of at least 5 N are reinforced, a period of transition will occur in which population characteristics of that lever-pressing operant are changing. If the new contingencies remain at 5 N, the population characteristics of that operant will stabilize and the force values of presses will differ from those that were observed before the contingency change.

Such shifts in the population characteristics of an operant might be compared to the changes in a species of moths observed near Manchester, England. *Biston betularia*, commonly referred to as the peppered moth, has two distinct appearances. Until the 18th century, the vastly more common appearance was a gray moth with mottled black coloration superimposed on its wings and body. This appearance cam-

ouflaged the moth when it clung to the bark of lichen-covered trees. *Biston betularia* also appeared as a completely black moth that was considered a rarity among British moth collectors of the time. These moths were rare because they had no camouflage and were more likely to be picked from the bark of trees by predatory birds. Thus, the population characteristics of the peppered moth species were predominantly "peppered." At the start of the Industrial Revolution, however, tree bark in the Manchester area became discolored by the black soot produced by coal-burning factories. The formerly rare black variant of *Biston betularia* was now at an advantage, because it was camouflaged against the soot-covered trees. Although the species itself did not change (just as the lever-pressing operant in the example above did not change), the population characteristics of the species changed dramatically under the new contingencies of survival (Wallace, King, & Sanders, 1981).

Not only do operants emerge from undifferentiated activity, but also more complex operants may evolve from simpler ones. More complex operant units do not require the disappearance of simpler units from which they emerged any more than the emergence of more complex forms (such as eukaryotes) required the disappearance of earlier forms (such as prokaryotes). The entire behavioral repertoire of a single living organism and the functional environment accounting for and sustaining its existence have been termed a *behavioral universe*—a parallel of the biological universe sustained by the Earth (Glenn, 1991).

In summary, species and operants evolve. Their members (organisms and responses) do not evolve but, rather, are the entities or units that provide the variation that makes differential selection possible. Organic evolutionary theory begins with observation of organisms and accounts for the origin of species, which are units that change over time as the result of the contingencies of natural selection. Similarly,

behavioral evolutionary theory begins with observation of responses and accounts for the origin of operants, which are units that change over time as the result of contingencies of reinforcement. In both cases, it is necessary to account for the continuity of the evolving entity. That continuity is provided by the functioning of the unit of retention and replication in the case of organic evolution. An analogous unit appears to be required in the case of the behavioral unit, and that is the topic to which we now turn.

RETENTION AND REPLICATION: PARALLEL UNITS?

It is critical to any evolutionary process that successive members of a lineage retain those characteristics that accounted for selection of their predecessors. Understanding of the unit of retention and replication—the gene—lagged far behind the initial statements (by Darwin and by Wallace) of the theory of evolution by natural selection (Mayr, 1982). The role of genetic transmission and mutation in organic evolution is now seen as complementary to the role of natural selection. In the early days of genetics, however, genetic theory was framed in such a way as to compete with the theory of natural selection. During the 1930s and 1940s the "modern synthesis" integrated Mendelian concepts of heritability and transmission and systematists' theory of natural selection in "a seemingly new theory of evolution . . . synthesized from the valid components of the previously feuding theories" (Mayr, 1980, p. ix). The evolutionary synthesis was unusual in that each of the theories did so much for the other, rather than one serving to support the other (Shapere, 1980, p. 392). Further, the synthesis not only integrated theories of two biological domains that previously had been viewed as competing but also provided a conceptual framework for virtually all biological sciences.

The systematist-naturalists and the geneticists appear to have distrusted one another's views in part because their methods differed. Specifically, the naturalists observed systematically and the geneticists experimented. But the fundamental difference may have been that they worked at different levels of analysis, and each group saw the creative force of evolution from its own perspective. The early geneticists were interested in inheritance and focused almost entirely on mechanisms of transmission and the primacy of mutation pressure in evolution. This placed the moving force of evolution inside the organism (specifically, in the genetic discontinuity resulting from mutations) and reduced selection's role to that of "eliminating deleterious mutations" (Mayr, 1982, p. 548). The naturalists were selectionists who were interested in changes and stabilities in the characteristics of natural populations of organisms across generations. They saw natural selection as the moving force behind these changes. When scientists interested in the genetic basis of evolution took up population thinking and began to study changes in gene frequencies in populations, the ground was laid for the evolutionary synthesis.

The current understanding is that organic evolution requires (a) retention across successive generations of genotypic characteristics, (b) variation among genotypic characteristics manifested in the phenotypes of a species, and (c) selection by the environment (evidenced by increases in frequency of some characteristics of a population and decreases in others). This view suggests that entities at three different levels of organization—genes, organisms, and species—are involved in the organic evolutionary process.

In previous sections we considered parallels between the organisms and species of organic evolution and the responses and operants of behavioral evolution. Retention and replication also appear to play a role in the ontogenic evolution of behavior. Behavior analysis is in a situation similar to that

of biology before the evolutionary synthesis and even before Mendel. However, behavioral evolutionary theorists have advantages in comparison with organic evolutionary theorists before the evolutionary synthesis. One advantage is that the experimental analysis of behavior has demonstrated behavioral selection in the laboratory, and thousands of technological applications have verified the principle in the everyday world. Thus, the phenomenon of selection is not contestable. As a further advantage, the explanatory structure of organic evolutionary theory may serve as a useful guide to theorists of evolutionary phenomena that occur with respect to other subject matters, including operant behavior. The latter advantage is what leads us to examine characteristics of the unit of retention and replication in organic evolutionary theory in order to direct our attention to possible parallels in the behavioral realm.

Replication and retention are related functions of the gene in evolution. The specific arrangement of chemicals is what is retained in genetic material across successive cells during ontogeny and across successive organisms during phylogeny. The existence of a species requires retention of the chemical code (arrangement) among organisms in a lineage. Retention of a chemical code across generations is possible only if faithful replication of the arrangement occurs as each new cell or organism arises.

In considering a behavioral analogue to the genetic unit of replication, an obvious candidate would be neurochemical events. As it happens, there are functional and structural similarities between genes and neurochemical events and between their respective relations with organisms and responses. Genes are chemical sequences that retain their patterns in a lineage of organisms; neurochemical sequences retain their patterns in a lineage of responses. The function of genes in a particular lineage is to maintain the characteristics selected as properties of

previous organisms in the lineage. The function of neurochemical events in a particular lineage is to maintain the characteristics selected as properties of previous responses in the lineage. The relation of genes to fully developed organisms is part to whole, as is the relation of neural events to full-blown responses.

If neural events are the behavioral unit of replication, then current behavior-analytic theory is in much the same position as evolutionary theory was before the rediscovery of Mendel and before Watson and Crick. Some understanding of the processes of behavior selection is at hand, but the mechanisms underlying retention of characteristics in a lineage are unknown, as is the material nature of the unit of replication. Proposing that the neurochemical event that occurs as part of an observable response is the behavioral unit of replication analogous to the gene has several implications. First, a complete scientific account of behavior must include an account of central nervous system processes (Skinner, 1974, p. 215). This is not to suggest that a science of behavior cannot advance without such knowledge. Rather, it suggests that neurophysiologists will identify the neurochemical processes involved in the behavior that enters into ontogenic selection contingencies. This information will supplement, not replace, principles of a science having as its subject matter behavior–environment relations, and it will make possible a synthesis of two related scientific disciplines.

A second implication of the proposed behavioral unit of replication is that some neurochemical event must be replicated faithfully between responses in an operant lineage. This implication seems to be counterintuitive when one considers that any two response instances of the same operant may be topographically dissimilar (e.g., lever presses made with a paw rather than a jaw). Before we dismiss neurochemical events as behavioral units of replication, however, let us consider ways in

which this biology–behavior comparison is apt. Thus far, we have argued that the operant is analogous to the species, and individual responses are analogous to organisms. If neurochemical events that occur in the nervous system are analogous to genes, then what would be required is that the neurochemical event associated with one response in a lineage generally would be replicated faithfully to initiate another response in that lineage. At present, the extent to which responses in an operant lineage possess neurochemical similarity is unknown.

Proposing a neural unit of replication for behavioral retention also has implications about the best way to identify more specifically the replicated neural event. There are at least two possible approaches. One method is to look inside the organism and identify the neural and biochemical events that may provide the material substrate responsible for retention and replication of ontogenic behavior. This approach might be viewed as paralleling the fields of cytology and molecular genetics. Another method is to develop a computer model of the behavioral gene that is consistent with known physiological processes and known behavioral processes. This approach might be akin to Watson and Crick's modeling of DNA.

One example of the “look inside the organism” approach is the theory of neuronal group selection (Edelman, 1987). Although Edelman's theory focuses primarily on the biological bases of perception, he links his theory of perceptual organization as a function of selection of neuronal groups to operant and respondent behavior. According to Edelman, individual organisms possess modally similar anatomical structures in the various areas of the brain. However, during embryonic development overlapping networks of neuronal groups are epigenetically (determined by genes and signals from gene-activating cell groups) formed with structural configurations unique to each individual. (Edelman cites inves-

tigations that have empirically identified several cell-adhesion molecules that are responsible for these arrangements of neuronal groups.) Although many neuronal groups may be functionally identical, they are structurally different from one another within the same organism. According to Edelman, there are more neuronal groups than can be activated by any given stimulus; thus, there are many concurrently existing instances of the variations on which selection can act. After birth, environmental stimuli may cause certain of these neuronal groups to fire with greater activity than other groups. Edelman suggested that this stimulus-induced increase of neuronal group activity causes a strengthening of the synaptic connections involved. Such strengthening constitutes selection of that group. Edelman (p. 181) cited several experimental studies describing synaptic modifications, but his account of how and when the synapses are strengthened remains largely hypothetical. Recent work by Stein, Xue, and Belluzzi (1994) provides preliminary information regarding biochemical processes that could be, in present terminology, involved in selection for neural events that function as the replicating cellular components of operant responses.

The second approach to identifying more specifically a behavioral unit of replication analogous to genes is to develop testable models of a mechanism of retention and replication. Such a model is that of Donahoe and his colleagues (Donahoe, Burgos, & Palmer, 1993; Donahoe & Palmer, 1989). The framework within which these researchers work is explicitly selectionism at the behavioral level of analysis. Beginning with what is known about behavior-environment relations, they model (via parallel distributed processing) known physiological processes to evaluate them as candidates for the behavioral gene. They then test the computer model for outcomes that are consistent with known outcomes of behavioral selection processes. If the behav-

ioral unit of replication is a neural event or mechanism, as suggested above, then the role of neural activity in behavior-analytic theory is parallel to the role of genetic replication in organic evolution. Neural activity may be conceived of as part of the behavioral instance itself; it is the initial part, which provides the neural pattern that gives rise to a response (comparable to a phenotype), and it is probably coded chemically and replicated across responses in a lineage.

Donahoe and Palmer (1989) have adapted many of the hypothesized mechanisms of neural pathway selection outlined in the adaptive network theory (McClelland, Rumelhart, & the PDP Research Group, 1986; Rumelhart, McClelland, & the PDP Research Group, 1986). Adaptive network theory uses parallel distributed processing in a computer as an analogue of the nervous system. This is said to be a fundamentally different kind of computer model than standard information processing models. The standard models assume that calculations according to prearranged, encoded rules are carried out by the brain in a manner similar to the way in which a computer's hard-wired rules for calculation control what happens to input to a computer's central processing unit. In the model developed by Donahoe and his colleagues, input units (analogous to receptors) are functionally connected to output units (analogous to effectors) via an interconnected network of hidden units (analogous to unobserved neurons). But the connections are acquired (not prewired) as a function of contingencies of behavioral selection.

One of the challenges of all selectionist accounts is to avoid hypotheses in which later events appear to affect earlier events—backwards causation. Although the adaptive network theory hypothesizes that connection strengths are modified in an output-unit to input-unit direction when outputs are discrepant with the appropriate output pattern (back propagation), there are at present no known neurophysiological

mechanisms that could accomplish such back propagation. However, back propagation may not be an issue in Donahoe and Palmer's theory. They have suggested that the input from behavioral consequences has a strengthening effect on all currently active networks. On any given occasion, many more networks are active than are required to meet the contingencies. Although many connections that are not critical to the output will be selected by the input generated by behavioral consequences, the critical antecedent input-output connections are necessary for reinforcement and the others are not. The contingency between the critical properties and reinforcement will result in a more consistent relation between the reinforcement and the critical property than between the reinforcement and noncritical properties. This is tantamount to selection for the critical properties. Connections with the most weight will be those that have led to reinforced outputs, and they will be those most likely to occur when antecedent input occurs.

The work of Donahoe and his colleagues is an example of model building, which is unusual in behavior-analytic theoretical development. Model building appears to be most useful when there are adequate technical tools as well as an adequate framework within which to develop the model. It remains to be seen whether parallel distributed processing is an adequate tool or whether behavior analysis can provide the framework to develop a workable model of behavioral retention.

The theoretical views of Donahoe and colleagues and Edelman do not appear to be incompatible. They may be working from different starting points, but both may aid in bridging the conceptual gap between principles of organic evolution and principles of behavioral evolution. Donahoe is explicitly developing a model based on known behavioral principles and is using parallel distributed computer processes to model known neural activity.

Edelman's theory is built up, somewhat more inductively, from experimental work at the cellular-molecular level. Either or both of these theories seem to have some potential for identifying the neural processes and biochemical structure of something akin to the gene in organic evolution.

CONCLUSION

Whether or not to conduct the analysis of acquired behavior within an explicitly evolutionary framework that is analogous to organic evolutionary theory is a question that has not yet been answered. Although *selectionist* is an adjective often applied to the behavior-analytic paradigm, the serious work of explicating what that means has barely begun. If behavior analysts gain nothing from continuing to work toward a fully developed selectionist paradigm, then such work will be likely to decrease in frequency. From the present perspective, the possible consequences seem to be worth the effort of working through the difficulties. Those consequences may include methodological and conceptual advances in behavior analysis. They may also place the behavior-analytic selectionist framework in the context of a general evolutionary paradigm that explains phenomena at numerous levels of analysis in terms of parallel evolutionary mechanisms that account for different phenomena at different levels.

REFERENCES

- Alessi, G. (1992). Models of proximate and ultimate causation in psychology. *American Psychologist*, 47, 1359-1370.
- Baum, W. M. (1994). *Understanding behaviorism: Science, behavior, and culture*. New York: HarperCollins College Publishers.
- Baum, W. M., & Heath, J. L. (1992). Behavioral explanations and intentional explanations in psychology. *American Psychologist*, 47, 1312-1317.
- Beatty, J. (1992). Fitness: Theoretical contexts. In E. F. Keller & E. A. Lloyd (Eds.), *Keywords in evolutionary biology* (pp. 115-119). Cambridge, MA: Harvard University Press.
- Brandon, R. N., & Burian, R. M. (1984). *Genes, organisms, populations: Controversies*

- over the units of selection. Cambridge, MA: MIT Press.
- Campbell, D. T. (1956). Adaptive behavior from random response. *Behavioral Science*, 1, 105-110.
- Catania, A. C. (1973). The concept of the operant in the analysis of behavior. *Behaviorism*, 1, 103-115.
- Catania, A. C. (1992). B. F. Skinner, organism. *American Psychologist*, 47, 1521-1530.
- Chiesa, M. (1992). Radical behaviorism and scientific frameworks: From mechanistic to relational accounts. *American Psychologist*, 47, 1287-1299.
- Darwin, C. (1958). *The origin of species*. New York: New American Library. (Original work published 1859)
- Dawkins, R. (1976). *The selfish gene*. New York: Oxford University Press.
- Dawkins, R. (1986). *The blind watchmaker*. New York: W. W. Norton.
- Donahoe, J. W., Burgos, J. E., & Palmer, D. C.. (1993). A selectionist approach to reinforcement. *Journal of the Experimental Analysis of Behavior*, 60, 17-40.
- Donahoe, J. W., & Palmer, D. C. (1989). The interpretation of complex human behavior: Some reactions to *Parallel Distributed Processing*. *Journal of the Experimental Analysis of Behavior*, 51, 399-416.
- Edelman, G. M. (1987). *Neural Darwinism*. New York: Basic Books.
- Endler, J. A. (1992). Natural selection: Current usages. In E. F. Keller & E. A. Lloyd (Eds.), *Keywords in evolutionary biology* (pp. 220-224). Cambridge, MA: Harvard University Press.
- Ghiselin, M. T. (1974). A radical solution to the species problem. *Systematic Zoology*, 23, 536-554.
- Glenn, S. S. (1991). Contingencies and meta-contingencies: Relations between behavioral, cultural, and biological evolution. In P. Lamal (Ed.), *Behavior analysis of societies and cultural practices* (pp. 39-73). Washington, DC: Hemisphere Press.
- Glenn, S. S., Ellis, J., & Greenspoon, J. (1992). On the revolutionary nature of the operant as a unit of behavioral selection. *American Psychologist*, 47, 1329-1336.
- Glenn, S. S., & Field, D. P. (1994). Functions of the environment in behavioral evolution. *The Behavior Analyst*, 17, 241-259.
- Hull, D. L. (1984). Units of evolution: A metaphysical essay. In R. N. Brandon & R. M. Burian (Eds.), *Genes, organisms, populations: Controversies over the units of selection* (pp. 142-160). Cambridge, MA: MIT Press.
- Hull, D. L. (1989). *The metaphysics of evolution*. Albany, NY: State University of New York Press.
- Keller, E. F. (1992). Fitness: Reproductive ambiguities. In E. F. Keller & E. A. Lloyd (Eds.), *Keywords in evolutionary biology* (pp. 120-121). Cambridge, MA: Harvard University Press.
- Lattal, K. A. (1992). B. F. Skinner and psychology: Introduction to the special issue. *American Psychologist*, 47, 1269-1272.
- Lee, V. L. (1988). *Beyond behaviorism*. Hillsdale, NJ: Erlbaum.
- Lee, V. L. (1994). Organisms, things done, and the fragmentation of psychology. *Behavior and Philosophy*, 22, 7-48.
- Mayr, E. (1980). Prologue: Some thoughts on the history of the evolutionary synthesis. In E. Mayr & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 1-48). Cambridge, MA: Harvard University Press.
- Mayr, E. (1982). *The growth of biological thought: Diversity, evolution, and inheritance*. Cambridge, MA: Harvard University Press.
- Mayr, E. (1988). *Toward a new philosophy of biology: Observations of an evolutionist*. Cambridge, MA: Harvard University Press.
- McClelland, J. L., Rumelhart, D. E., & the PDP Research Group. (Eds.). (1986). *Parallel distributed processing: Explorations in the microstructure of cognition: Vol. 2. Psychological and biological models*. Cambridge, MA: MIT Press.
- Mechner, F. (1992). *Behavior monographs: The revealed operant: A way to study the characteristics of individual occurrences of operant responses* (2nd ed.). Cambridge, MA: Cambridge Center for Behavioral Studies.
- Palmer, D. C., & Donahoe, J. W. (1992). Essentialism and selectionism in cognitive science and behavior analysis. *American Psychologist*, 47, 1344-1358.
- Paul, D. (1992). Fitness: Historical perspectives. In E. F. Keller & E. A. Lloyd (Eds.), *Keywords in evolutionary biology* (pp. 112-114). Cambridge, MA: Harvard University Press.
- Ringen, J. D. (1993). Adaptation, teleology, and selection by consequences. *Journal of the Experimental Analysis of Behavior*, 60, 3-15.
- Rumelhart, D. E., McClelland, J. L., & the PDP Research Group. (Eds.). (1986). *Parallel distributed processing: Explorations in the microstructure of cognition: Vol. 1. Foundations*. Cambridge, MA: MIT Press.
- Schick, K. (1971). Operants. *Journal of the Experimental Analysis of Behavior*, 15, 413-423.
- Shapere, D. (1980). The meaning of the evolutionary synthesis. In E. Mayr & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 388-398). Cambridge, MA: Harvard University Press.
- Skinner, B. F. (1938). *The behavior of organisms*. Englewood Cliffs, NJ: Prentice Hall.
- Skinner, B. F. (1953). *Science and human behavior*. New York: Free Press.
- Skinner, B. F. (1957). *Verbal behavior*. New York: Appleton-Century-Crofts.
- Skinner, B. F. (1972). Two types of conditioned reflex: A reply to Konorski and Miller. In *Cumulative record* (3rd ed., pp. 489-497). (Orig-

- inally published in *The Journal of General Psychology*, 16, 272–279)
- Skinner, B. F. (1974). *About behaviorism*. New York: Knopf.
- Skinner, B. F. (1981). Selection by consequences. *Science*, 213, 501–504.
- Skinner, B. F. (1984). The evolution of behavior. *Journal of the Experimental Analysis of Behavior*, 41, 217–221.
- Skinner, B. F. (1986). The evolution of verbal behavior. *Journal of the Experimental Analysis of Behavior*, 45, 115–122.
- Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus*. Cambridge, MA: MIT Press.
- Staddon, J. E. R. (1973). On the notion of cause, with applications to behaviorism. *Behaviorism*, 1, 25–63.
- Stein, L., Xue, B. G., & Belluzzi, J. D. (1994). In vitro reinforcement of hippocampal bursting: A search for Skinner's atom of behavior. *Journal of the Experimental Analysis of Behavior*, 61, 155–168.
- Wallace, R. A., King, J. L., & Sanders, G. P. (1981). *Biology: The science of life*. Glenview, IL: Scott Foresman.
- Wilson, E. O. (1975). *Sociobiology: The abridged edition*. Cambridge, MA: Harvard University Press.